Reference: *Biol. Bull.*, **147**: 95–104. (August, 1974)

LOCOMOTION OF THE HOLOTHURIAN *EUAPTA LAPPA* AND REDEFINITION OF PERISTALSIS

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Observation of the holothurian *Euapta lappa* (J. Muller, 1853) reveals locomotory waves that are unlike any previously described. According to the terminology of Vles (1907), the wave is direct rather than retrograde, meaning that it moves in the same direction as the animal—in this case, anteriorly. In *Euapta,* the wave is peristaltic and involves no elevation of the body cylinder's major axis. Direct peristaltic locomotory waves, previously described in the holothurians *Stichopus panimensis* and *Astichopus multifidus* have an arch above the substratum formed by the localized temporary elevation of the body cylinder's major axis (Parker, 1921; Glynn, 1965). Although retrograde waves in wormlike animals are well understood (Gray and Lissman, 1938; Clark, 1964), direct locomotory waves are less well known (Elder, 1973a, 1973b). This paper presents the first description of locomotion in *Euapta* and a resolution of the ambiguity of the term "peristalsis." "Peristalsis" is herein redefined as any muscular contraction moving along a radially flexible tube in such a way that each component wave of circular, longitudinal or oblique muscular contraction is preceded or followed by a period of relative relaxation of all similarly oriented muscle within a given tubular segment. A classification of some known types of peristalsis is also presented.

The Experimental Animal and Methods

Euapta lappa is an apodous holothurian with a wormlike appearance. The animal has an extremely flexible body which may attain an extended length of 1 m and a diameter of 2–4 cm. If disturbed, however, *Euapta* can contract regions of the body to about one third their extended lengths. The anterior end has a circumoral ring of 15 pinnate tentacles and the body cylinder, in a condition of tonus (resting muscular tension), has five radially symmetric rows of outpocketings called warts (Fig. 1). The animal has both circular and longitudinal muscles; the former are a continuous tube throughout the body; the latter are restricted to 5 strips arranged in radial symmetry and extending the length of the body. The animal's body surface is covered with many anchor-shaped calcareous ossicles (Hyman, 1955) approximately 0.4 mm long which aid in attachment to the substratum.

Specimens were obtained from Tropical Atlantic Marine Specimens, Big Pine Key, Florida, and kept in a 25 gallon aquarium filled with recirculated artificial sea water ("Instant Ocean") on a crushed shell substratum. Observation was the main technique and a continuous-feeding 35 mm movie camera (Grass) was used to record and "slow down" the motion. The camera's shutter was always open and images were formed by the flashing of a stroboscopic light in a dark room. For filming, the animal was transferred to a smaller and narrower tank provided with a centimeter grid as a background for reference. Living body wall was examined with a Wild M-5 dissecting microscope with polarizing attachments.

Results

Warts (Fig. 1) are not permanent structures. Individual warts may be observed to shift or "slide" slightly along the major body axis, to increase or decrease in size and to divide into two smaller warts or merge to form a larger wart. Warts do not divide or merge circumferentially. A single wart will collapse when its apex is pinched with forceps. Animals anesthetized with magnesium salts have a body cylinder of greater average diameter with no warts.

Histological preparations failed to reveal any morphologically distinct structure that might account for the warts. In living animals, a number of warts were tagged by threading them with a suture. But subsequent vivisection did not reveal any distinct correlated structures except that tags were always between two adjacent strips of longitudinal muscle (Fig. 1a). The five relatively narrow strips of longitudinal muscles are separated by five relatively wider strips of body wall lacking longitudinal muscles. This pattern of longitudinal muscle is superimposed on the continuous circular muscle layer.

Thus, we conclude that warts in *Euapta* and probably those in other similar apodous holothurians are not specific morphologically distinct points or structures as is suggested by other writers (Hyman, 1955). Instead, warts appear to be areas of limited contraction of circular muscle bounded by regions of greater degree of contraction of circular muscles. These holothurian warts then are analogous to the haustrations of the vertebrate large intestine (Guyton, 1971). Divisions of warts are effected by contraction of additional circular muscles, and merging occurs when a contracted ring of circular muscle relaxes.

The locomotory wave (Fig. 1b)

By observing the distance between points on the body wall, it is possible to tell when longitudinal or circular muscles are contracting. As the direct locomotory wave passes along a section of the body wall, contraction of longitudinal muscles (B) is the first evident occurrence. Warts and recognizable pigmented points on the body wall come closer together longitudinally in an accordion-like effect. Then, while longitudinal contraction is still under way, circular contraction occurs (C) as is evidenced by the decrease in diameter of the body cylinder and the "flattening" of warts. This is followed by relaxation and extension of all body wall musculature (D) so that the entire body wall bulges outward. Expansion is follower by a return to the original tonus (E).

Each locomotory wave starts at the posterior end of the animal by the same sequence of longitudinal and circular contraction. Each part of the body wall advances while under longitudinal contraction. The major axis of the body is not raised in the formation of an arch but rather an arch is formed by a decrease in diameter of the body cylinder. The body axis does not change its position. Con-

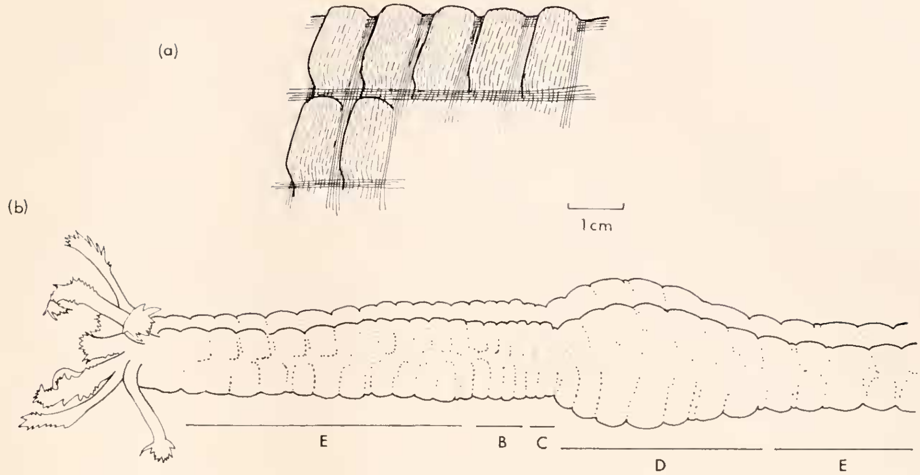

FIGURE 1. Diagrams showing the external shape of the apodous holothurian *Euapta lappa.* (a) Seven warts are shown with the muscles that delineate them: solid lines indicate muscles in state of tonus; broken lines indicate relaxed circular muscles; (b) body of *Euapta* with a direct overlapping peristaltic wave passing from right to left; B, initial contraction of longitudinal muscle; C, contraction of circular muscle and further longitudinal muscle contractions; D, relaxation of all muscles: body wall distended by coelomic pressure; E, state of tonus.

traction of circular muscles releases the body wall from its attachment to the substratum, thus facilitating forward movement.

The *direct overlapping peristalsis* described above is the most common method of locomotion in *Euapta,* but variations do exist as a result of the reduction or complete suppression of some of its components. One type of wave, *direct longitudinal peristalsis,* is characterized by longitudinal muscular contractions as observed in the direct overlapping peristalsis, but there is no accompanying wave of circular contraction. Direct longitudinal peristalsis is observed when the animal crawls across smooth glass surfaces and when it is climbing up a vertical aquarium wall clinging by its tentacles with part or all of its body hanging free below. Sometimes this direct longitudinal paristalsis passes along a body cylinder which is in a tonus state of circular contraction. At other times the body cylinder is constricted throughout part or all of its length by continuous contraction of circular muscles. This obliterates all warts and holds the body diameter constant while waves of only longitudinal contraction pass along the body. In these two cases of waves of longitudinal muscle contraction passing along a body cylinder of unchanging diameter, it is clear that friction is minimal and offers little help or hindrance to forward motion. Direct longitudinal peristalsis is further considered in the discussion.

Another type, *direct overlapping partially circular peristalsis,* has normal contraction of longitudinal muscle but only the two ventral-most warts are retracted, as opposed to the full circumferential contraction by circular muscles seen in direct overlapping peristalsis. This wave of incomplete circular muscle contraction was observed on only two occasions and was never recorded on film.

There is another wave which may be of interest. Viewed infrequently while the animal is resting, this *circular contraction peristalsis* is a wave of contraction of only circular muscles that seems to have no locomotory function.

These different waves are not necessarily mutually exclusive behavioral events. A wave in *Euapta* may start as a certain type; by the time it reaches the anterior end it may be modified to one of its variations. Intermediate forms exist.

Upon first viewing *Euapta* move by direct overlapping peristalsis, it may be apparent why longitudinal contraction advances a more posterior point rather than pulling an anterior point posteriorly. Obviously circular contraction raises the body wall from the substratum while the still-attached body wall anterior to the locomotory wave acts as a fixed point of attachment. Thus, longitudinal contraction will move detached points forward toward the fixed point. In addition, *Euapta's* calcareous ossicles are believed to be so situated that they catch the substratum when pulled posteriorly and release their hold when pulled anteriorly (Hyman, 1955). It appears that opportunities for catching onto the substratum are maximum when the body is maximally inflated and the epidermis is stretched tightly over the ossicles. Portions of the body anterior to a locomotory wave are under slight longitudinal stretch which is increased by the approaching longitudinal contraction. Accordingly, these regions, just anterior to a locomotory wave, will have their ossicles well protruded and attached to the substratum, each forming a fixed point. During locomotion the tentacles also act as fixed points at the anterior end. Each tentacle in turn sweeps from its extended position in front of the animal, backward toward the mouth. It then reaches forward and attaches to the substratum creating a fixed point. A tentacle may subsequently detach and sweep back toward the mouth or it may first contract longitudinally and take up any "slack" left by a peristaltic wave before detaching.

Discussion

When *Euapta* hangs from the vertical glass wall of an aquarium, the tentacles are the only fixed points of attachment. In this situation direct longitudinal peristalsis continues to serve a locomotory function. Each such wave gives the animal a boost as it climbs the glass. Each wave begins by pulling the posterior end upward and forward. The region of longitudinal compression thus formed is propagated anteriorly. This situation is analogous to that of a "slinky" toy, hanging vertically from one end. A "slinky" toy is a long easily extensible spring with a small spring constant, K, according to the equation $F = -KX$ where F is the force generated by the spring and X is the linear displacement of an end of the spring stretched from its resting length. Such springs hung vertically will elongate to many times their resting length due to gravity alone.

If the lower end of a vertically hung "slinky" is pushed up one foot and released, a wave of compression is formed which travels upward while the lower end of the spring begins to fall back down. The upward travelling wave of longitudinal compression, upon reaching the upper end, provides an upward force opposing the downward force of gravity. Meanwhile, as the lower end which was lifted up and then released begins to fall back down, the downward force of gravity acting upon the mass of the spring at the lower end is manifest in the motion of the falling segment of spring. Thus, as long as the lower part of the spring is still falling, the weight of this lower part of the "slinky" is not borne by a point of attachment at the upper end. However, the lower end of the spring is brought to an abrupt stop and would need to be stretched to continue any further downward motion. The point of attachment now must provide an upward force equal and opposite to the force of the downward acceleration of gravity acting upon the mass of the lower end of the spring; the point of attachment reassumes support of the weight of the lower end of the spring. In addition, the fixed point of attachment must momentarily supply another upward force: one that is not even required when the fixed point is supporting the whole body weight. This upward force is needed to cause the rapid deceleration (an upward acceleration) of the falling mass of the lower end of the spring as it comes to a stop.

In the instance of *Euapta* hanging and climbing by its tentacles, a wave of longitudinal compression reaches the anterior end, providing an upward force. This force causes an upward displacement of the anterior end. The tentacles for a moment do not have to support the full weight of the body. While some of the tentacles maintain their hold, others reach forward and secure a new hold before they must resume full support of the body mass and absorb the momentum of the falling lower body region.

Definitions of "peristalsis" found in dictionaries are contradictory and confusing. We have given a description of the direct peristaltic locomotory waves found in *Euapta*, which are very different from the direct peristaltic locomotory waves described for *Astichopus* by Glynn (1965). Parker (1921) did not use the term "peristalsis" to describe the wave he observed in *Stichopus* but accounts of his work by text writers (Clark, 1964) indicate that the wave he observed is considered by them to be peristaltic. Elder (1973b) states that locomotion in the apodous holothurian *Leptosynapta* is achieved by means of direct peristaltic waves involving simultaneous longitudinal and circular muscle contraction. Duncan and Pickwell (1939, page 141) described the telescopic locomotion of dipteran larvae as being "similar to peristalsis." A more recent reviewer, (Hughes, 1965, page 233) however considers apodous larvae to be "entirely dependent on peristaltic movements of the body for propulsion." Direct pedal locomotory waves of gastropods and the direct peristaltic locomotory waves of *Euapta* both function by similar mechanisms. In each case the ventrum is lifted from the substratum and then advanced by contraction of longitudinal muscles. Yet the latter is termed peristaltic and the former is not. All too often an author, upon identifying a wave as peristaltic, believes he has adequately characterized the wave. Some authors (Code and Carlson, 1968; and Ritchie, Truelove, Ardran and Tuckey, 1971) working with mammalian intestinal contractions; seem to have adopted the definition of peristalsis as a propulsive wave of contraction of part or all of the circular muscle. This working definition, however, excludes contractions observed in invertebrates which have long been termed peristaltic.

Mammalian gastroenterologists have what is perhaps an even more confusing terminology problem. Balloons and open-tipped catheters inserted into the mammalian gastrointestinal tract yield four distinct types of pressure wave recordings. These recordings include pressure changes caused by peristaltic as well as nonperistaltic contractions. Two of these four classifications differ only in the amplitude of their fluctuation (Hightower, 1968). There is no clear accepted correlation between types of pressure recordings and the varied types of gastrointestinal movement recognized by direct observation and cineradiography; segmenting movements, pendulum movements, peristalsis and peristaltic rushes. Some authors believe that the pendulum movements are identical with segmenting contraction. Pressure recording classifications tell us nothing about the mechanical process involved and they are valued mostly as diagnostic tools in medicine.

Most important to our discussion is the fact that there is still disagreement as to the contraction sequence of circular and longitudinal muscle components in mammalian intestinal peristalsis (Bortoff and Ghalib, 1972; Gonella, 1972; Raiford and Mulinos, 1934; Bayliss and Starling, 1899; and Wood and Perkins, 1970). Obviously some standardization of terminology is necessary. The following, then, is an attempt to construct a useful definition of "peristalsis" consistent with its past and present usage.

Peristalsis is the phenomenon of any muscular contraction moving along a radially flexible tube in such a way that each component wave of circular, longitudinal or oblique muscular contraction is preceded and/or followed by a period of relative relaxation of all similarly oriented muscle within a given tubular segment. The meaning of this definition is not changed if the word "relaxation" is replaced by "contraction" and each "contraction" is replaced by "relaxation."

In any form of peristalsis, any two tubular segments are subject to a sequence of qualitatively identical force vectors. Furthermore, in locomotory peristalsis, each region of the body must, at some time during or between the passages of waves, have no forward motion. This is in contrast to the continuous undulatory locomotory mechanisms of fishes or the rectilinear progression of the boa constrictor (Gray, 1968), where the body moves as a unit and at a constant rate.

This definition is consistent with current and past use of the term "peristalsis" and includes the propagated waves of contraction found in vertebrate intestine, the retrograde locomotory waves found in earthworms and other coelomates, the locomotory waves characteristic of lepidopterous caterpillars (Barth, 1937), the direct locomotory waves of both dipteran larvae and *Euapta* and undoubtedly many more mechanisms of locomotion. Although the definition includes the locomotory waves of lepidopterous caterpillars, it excludes the sinusoidal locomotory waves of *Nereis* which involve alternating component waves of longitudinal contraction on opposite sides of the body cylinder (Gray, 1968). The definition also excludes swimming movements of leeches and fish, pedal locomotory waves, and the serpentine, concertine, crotaline and rectilinear movements of snakes (Gray, 1968). The peculiar swimming movements of young adult *Leptosynapta* are similarly excluded (Costello, 1946). The term, however, remains broadly applicable and an attempt to classify the types of peristalsis seems appropriate.

In the following classification of peristaltic types, all locomotory peristalsis will be classified as either direct or retrograde. The word "locomotory" is omitted to avoid verbosity. Only the names of non-locomotory waves will be without this direct versus retrograde distinction. Although some types of non-locomotory peristalsis may be mechanistically equated with forms of locomotory peristalsis, this distinction between locomotory and non-locomotory peristalsis is useful.

Transportive peristalsis as seen in the vertebrate intestine has not been fully characterized. Kosterlitz (1968), Raiford and Mulinas (1934), Wood and Perkins (1970) and Gonella (1972) believe longitudinal and circular muscle contract sequentially. Thomas and Baldwin (1971), Bortoff and Ghalib (1972) and Bayliss and Starling (1899) propose a simultaneous contraction of both circular and longitudinal muscle followed by a subsequent simultaneous relaxation.

A *Circular contraction peristaltic* wave is a wave of contraction of circular muscles only. *Euapta* has such a wave, and it cannot serve to pull the animal forward. It may serve some other purpose, as in the "ring of constriction" in *Thyone* (Pearse, 1908, page 266) which facilitates the detachment of tube feet from the substratum. The peristaltic wave described by Yamanouchi (1929) and Crozier (1915) may be circular contraction peristalsis. Yamanouchi's paper includes a diagram depicting a wave very much like the direct overlapping peristalsis of *Euapta* and he cites Crozier as having already described this type of wave in detail. Crozier, however, describes peristalsis in *Holothuria surinamensis* originating at any section of the body and slowly travelling either anteriorly or posteriorly. The body is not raised above the substratum and movement is accomplished primarily by the action of pedicles. Buccal tentacles and contraction of the body musculature play secondary roles in this locomotion.

Partially circular relaxation peristalsis consists of a wave of relaxation passing as an incomplete ring along the circular musculature. Coelomic fluid pressure causes distension at the point of relaxation. The worm *Arenicola* seems to use this type of wave to irrigate its' tubule although the role of longitudinal musculature is not delineated (Wells, 1961). In the case of *Arenicola* the wave of relaxation is restricted to the dorsal region. A wave occludes the space between the worm's dorsal surface and the walls of the tubule thus pushing water in front of it.

Longitudinal contraction peristalsis is a wave of contraction of only longitudinal muscles that is unrelated to locomotion. Sabella uses such a wave to irrigate its tubule (Mettam, 1969). Starting at one end of the body, a wave of longitudinal contraction shortens constant volume segments causing dilation. The dilated region closely fits the smooth tubule and the propagated wave acts like a "piston" traveling the length of the tubule and pushing water in front of it. Sabella's "piston" is able to move with minimal frictional resistance since parapodia are retracted and abundant mucous glands provide lubrication. Narrow elongated segments grip the tubule wall with extended parapodia.

Direct longitudinal peristalsis refers to waves of contraction of only longitudinal muscles travelling in the same direction as the animal. *Euapta* is capable of this wave type.

Direct arching peristalsis is observed in some lepidopterous caterpillars (Barth, 1937). Basically, a wave of contraction passes anteriorly along the dorsal longitudinal musculature and is followed by a wave of contraction of the dorso-ventral musculature. As the dorso-ventral musculature subsequently relaxes, a wave of contraction of the ventral musculature passes along the body tube.

Although they haven't been analyzed into their component muscular contractions, similarly described waves have been reported in holothurians. Parker (1921, page 205) reports a direct muscular wave in *Stichopus* which "resembles superficially the locomotion of a gigantic caterpillar." Glynn (1965, page 112) describes *Astichopus's* peristalsis in which "the posterior end is first elevated two to four centimeters from the substratum and then the wave moves forward forming an arch 2 cm high between ventrum and the underlying surface."

Direct overlapping peristalsis is the locomotory mechanism most frequently observed in *Euapta.* This type of peristalsis moves in the same direction as the animal. A wave of contraction of the longitudinal musculature passes along the body and during the latter part of its duration, occurs simultaneously with a wave of contraction of the circular muscles. Relaxation of circular and longitudinal muscles occurs simultaneously. The body cylinder's major axis is not elevated. In the burrowing polychaete *Polyphysia crassa* (Elder, 1973a) and in the apodous holothurian *Leptosynapta* (Elder, 1973b), the contractions of circular and longitudinal muscules appear to be simultaneous.

Direct overlapping partially circular peristalsis as demonstrated in *Euapta* is similar to direct overlapping peristalsis, differing only in the radial extent of circular contraction. In the former, contraction of circular musculature does not involve entire bands or rings of circular muscle as is the case for the latter.

Telescopic locomotion (Duncan and Pickwell, 1939), a *direct non-overlapping peristalsis* has been reported in some dipteran larvae. A direct wave of circular muscle contraction increases the pressure of the body fluids thus causing the body to lengthen and, pushing against a posterior fixed point, moves the head forward. While the head anchors itself to the substratum, a direct wave of contraction of longitudinal muscles then pulls the posterior regions forward. This appears similar to the burrowing activity observed in *Arenicola* (Truman, 1966).

Direct dilation peristalsis is reported in *Arenicola* (Mettam, 1969). In this type of locomotion (Wells, 1949) a direct wave simultaneously relaxes both circular and longitudinal musculature. Coelomic fluid pressure in the relaxed segment causes the body wall to dilate and contact the sides of the tubule, thus acting as a fixed point. Once the wave of relaxation passes, both circular and longitudinal muscle return to tonus. As the longitudinal muscle returns to tonus, longitudinal shortening pulls the tubular segment toward the fixed point which has in the meantime moved anteriorly.

Retrograde non-overlapping peristalsis is the method of locomotion of earthworms and is described in detail by Gray and Lissman (1938), Clark (1964) and Child (1901). Waves of contraction of longitudinal muscles pass posteriorly causing dilation of the body cylinder. A wave of contraction of circular muscles follows immediately, but does not overlap the longitudinal wave, and causes elongation of the body cylinder as well as causing it to push forward from more posterior fixed points. In some cases, as in earthworms, fixed points are provided by the increased body diameter. In some animals, fixed points are provided by other means of attachment. In the leech, for example, the suckers at each end of the body alternately serve as fixed points.

Retrograde dilation peristalsis is reported in Sabella (Mettam, 1969). A retrograde wave of contraction passes along the longitudinal muscle as the segmental volume is kept constant. Longitudinal shortening pulls a segment anteriorly toward a fixed point. Continued longitudinal shortening dilates the segment until it become wedged against the tubule walls and itself acts as a fixed point. After a wave of longitudinal contraction, a segment extends anteriorly.

These classes of peristalsis are not intended to be considered as the only possible classes. They do represent the different forms of muscular waves considered to be peristaltic that we have encountered in the literature.

Apodous holothurians comprise an unusual adaptation of hydrostatic skeletons.

Most animals that move by peristalsis have relatively thick body walls and high internal hydrostatic pressures. *Euapta* and other apodous holothurians are low pressure creatures whose body wall is so thin that it is ruptured by the weight of coelomic fluid if the animal is lifted into the air by one end. The Caribbean *Euapta* and the Pacific *Opheodesoma* live completely exposed on reef tops among corals and attached algae. They must normally be constant volume hydrostats—as are burrowing annelids. But these holothurians may, at any one time, contract the longitudinal muscles in the entire front (or rear) 2/3 of the animal and force the coelomic fluid into the remaining 1/3. This inflated 1/3 will have a larger diameter and no warts. Even those polychaetes that have incomplete septa cannot change their dimensions to this extent. As a result of their ability to change dimensions drastically, apodous holothurians can pass through cracks or holes in the substrate that are less than 1/3 their diameter. This recalls similar behavior of *Peripatus* (Manton, 1958) which is similarly correlated with lack of effective septa.

The structural dependence of holothurian warts upon hydrostatic pressure is reminiscent of the tube feet found in many other echinoderms. Yet while a retracted tube foot is still an anatomically identifiable structure, a flattened wart on *Euapta* is totally indistinguisable from adjacent regions of body wall.

We would like to thank Mrs. W. R. Heffernan for her selfless assistance in repeated typing and editing of the manuscript.

Summary

1. The apodous holothurian, *Euapta lappa,* demonstrates four types of peristalsis. Direct overlapping peristalsis in which circular and longitudinal muscle components overlap is the most common. Other types are characterized by (a) being of longitudinal muscles only, (b) lack of circular muscle contraction along one side of the body and (c) being of circular muscles only (nonlocomotory).

2. "Warts" in apodous holothurians are not discrete structures but are areas of the body wall delimited by temporary contraction of circular muscles.

3. Peristalsis is defined as any muscular contraction moving along a radially flexible tube such that each component wave of circular, longitudinal or oblique muscle contraction is preceded or followed by a period of relative relaxation of all similarly oriented muscle. Definitions and nomenclature are given for 8 locomotory and 4 non-locomotory types of peristalsis.

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